

## DIVDROP analysis – a new method for the interpretation of species importance in diversity changes

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**Abstract** — With the aid of a new method named DIVDROP, the process of changes in diversity can be analysed as a trend. The importance of the species can be estimated in shaping the great changes in the value of the diversity. The method is demonstrated on two vegetational examples: 1. on algological samples taken in 30 consecutive days from Lake Balaton and 2. on 20 consecutive relevés of *Salvia-Festucetum* along a forest road. In both cases a large proportion of diversity changes proved to be satisfactory explained by using the DIVDROP method. A computer programme written in FORTRAN-IV language is part of the BP programme package of the Hungarian Natural History Museum. With 12 figures.

**Introduction** — Any student working on diversity studies of communities often speculates on the problem why the value of diversity is so high or low and what species are more or less important in forming it. The question arises mainly in cases where the individuals (relevés, samples, etc.) are part of some kind of series (time series; a row of sampling plots or quadrates; sampling plots or quadrates along any kind of gradients, etc.). In studies like these diversity often has a characteristic trend along the series, with the existence of local maxima and minima. One would like to answer the question whether there are a few (mainly one or two) species responsible to various extent for this trend or not. To solve these problems we propose a new method, the DIVDROP analysis.

### The DIVDROP method

The method itself can be adapted to any weighted measure of diversity (cf. PIELOU 1975), though we have used the Shannon index with a logarithm based to 2. This index has a lot of advantages and is widely used (cf. HAJDU 1977, 1978). The essence of the method is that we remove the data of the species to be analysed from the whole matrix of data and calculate the diversity values again. If we compare these values with the original values of diversity we will get useful information about the importance of the given species. In symbols:

$$H'' = - \sum_{i=1}^s \frac{a_i}{N} \log_2 \frac{a_i}{N} \quad (\text{SHANNON 1948})$$

where  $a_i$  is the quantity (cover, number, biomass, etc.) of the  $i$ -th species;  $s$  is the number of species in the individual; and

$$N = \sum_{i=1}^s a_i.$$

This way the resulting “reduced” diversity will be:

$$H''\text{red}_k = - \sum_{i=1}^{k-1} \frac{a_i}{N-a_k} \log_2 \frac{a_i}{N-a_k} - \sum_{i=k+1}^s \frac{a_i}{N-a_k} \log_2 \frac{a_i}{N-a_k}$$

where  $H''\text{red}_k$  is the “reduced” diversity omitting the  $k$ -th species.

A computer programme was written in FORTRAN-IV language to implement this analysis. The programme, named DIVDROP, has been incorporated into the BP programme package of the Hungarian Natural History Museum which runs on the CDC-3300 machine of the Hungarian Academy of Sciences under Master 4.1.

Usually the number of species is fairly large in most of cases and only several species have any remarkable effect on diversity. It is not worth having the results printed out for all the species as it would be a waste of paper, so an algorithm was built into the programme to choose the species we are interested in. The method itself is a practical one without any theoretical consideration. Let

$$\Delta H''_{jk} = H''_j - H''_{\text{red}_{jk}},$$

where  $j$  is the serial number of the individual,  $\Delta H''_{jk}$  is the diversity difference of the  $j$ -th individual omitting the  $k$ -th species. — One species might be of importance in following two cases:

1. if the average diversity difference per individual is great enough (the species has an overall effect or a large local effect), i.e.

$$\frac{1}{N} \sum_{j=1}^n |\Delta H''_{jk}| > c_s$$

where  $n$  is the number of individuals in the data series,  $c_s$  is the critical level for this series (in our study  $c_s = 0.05$  proved to be efficient);

2. if the average diversity difference per individual is small but at least one single value of  $\Delta H''_{jk}$  is great enough, i.e.

$$\frac{1}{N} \sum_{j=1}^n |\Delta H''_{jk}| < c_s, \text{ but } \frac{\max |\Delta H''_{jk}|}{H''_j} > c_i,$$

where  $c_i$  is the critical level for the individuals (in our study  $c_i = 0.05$  proved to be efficient).

### The hydrobiological example

Recently, studies on the seasonal succession of phytoplankton communities and analyses on the roles of single species have become some of the most frequented subjects of hydrobiological studies (e. g. LYNCH & SHAPIRO 1981, SOMMER 1981, WALL & BRIAND 1980, WHITING et al. 1978). During an annual cycle phytoplankton communities seldom appear as discrete units. In most cases, mainly in shallow lakes, closely attached communities integrate one with another through time and often exhibit no distinct boundaries between them. A special difficulty is that the changes in abundance of about hundred or more species of algae must usually be studied. That was the case in a day-to-day study carried out in Lake Balaton in the summer of 1978 (PADISÁK 1980).

During the thirty-day study 134 species of algae were found in the samples. Most of them may be considered as rare with an average number over the month below  $300 \text{ ind} \cdot 1^{-1}$  (frequency measure: 1), 41 species had an average between 300 and 3000; 29 between 3000 and 20,000; 12 between 20,000 and 80,000 and only 2 above 80,000  $\text{ind} \cdot 1^{-1}$  (frequency measures: 2, 3, 4 and 5, respectively). Ordering the species based on their decreasing number seems to be a convenient way to estimate their importance in the community, but it may lead to a considerable loss of information because a heavy storm broke out at the middle of the study period which was followed by characteristic changes in the population dynamics of the most abundant species. The diversity also changed in correlation with that storm. Its changes could not be completely explained as based on the abundance patterns of the species. DIV-DROP analysis was more successful in this case.

Species having a frequency measure of 1, 2 or 3 had no significant effect on diversity changes, their (nevertheless always positive) effect was under the critical level ( $c_s = 0.05$ ), except for three species. All the species with a frequency measure of 4 had an average diversity difference above the critical level as well. After removing them from the data-set the diversity decreased except for *Nitschia* sp. 1., removing its data an increase in diversity was noted in two samples (Fig. 1A). The species mentioned above can be divided into three

groups according to their DIVDROP effect. There are two species among them which had an equal, overall effect through the 30 days. Further two species had a nearly continuous decreasing importance, and nine species had an increase effect on diversity right after the storm. Representatives for these three cases are given in Figs 1B, C, D. Only two species: *Aphanizomenon flos-aquae* RALFS ex BORN. et FLAH. f. *klebahnii* ELENK. and *Coelosphaerium kuetzingianum* NÄG. have a frequency measure of 5. Their removal from the data-set usually caused a great change (mainly increase) in diversity (Fig. 1E, F).

Shannon diversity (Fig. 2) shows a roughly constant decrease with a maximum around 9th day of the study period. This trend cannot be due to any decrease in the number of species coexisting day to day, for the number of species slightly but continuously increased during the 30 consecutive days (Fig. 3). Most of the species above  $c_s = 0.05$  had positive effect on diversity so they also could not be responsible for such a trend. There were only three species (Figs 1A, E, F) which might be suspected to have caused this trend. *Nitschia* sp. 1. does not seem likely to have been responsible for the trend because we could observe only two days when it had negative effect on diversity. In Fig 4A, B the DIVDROP effects of *Aphanizomenon flos-aquae* f. *klebahnii* and *Coelosphaerium kuetzingianum* are plotted against Shannon diversity. As it can fairly well be seen, the rise in diversity (the local maximum around 3 August) might have been caused by a decreasing negative effect of *Coelosphaerium kuetzingianum*. After this slight peak a continuous decrease in diversity can be observed. First, on 6–8 August *Aphanizomenon flos-aquae* f. *klebahnii* was the species which was responsible for that, then, between 9 and 14 August *Coelosphaerium kuetzingianum*. So the trend in diversity can satisfactorily be explained through the patterns of these two species till 14 August. The local minimum of diversity around 16 August fits well to that of in number of species (cf. Fig. 3). The following decrease in diversity could not be explained by any single effect, it might have been an additive result of many small effects, e. g. the pattern in the number of species or the decreasing positive effect of less important species (see the *Cosmarium bioculatum* like pattern, Fig. 1).

So the storm which broke out on 9 August had a profound effect on the phytoplankton community. Before the storm *Aphanizomenon flos-aquae* f. *klebahnii* began to be overwhelmingly predominant, then a crash occurred correlated with the storm and the community became predominated by another species of blue-green algae. The effect of the storm is also obvious considering the importance patterns of the less dominant species.

### The terrestrial example

20 consecutive relevés of *Salvio (nutanti-nemorosae)-Festucetum rupicolae* were recorded along a forest-road in N-Hungary (SZUJKÓ-LACZA & RAJČY 1983). The trend of changes in diversity along the relevé series can be seen in Fig. 5. Relevés 1 and 2 had the highest diversity values. They were very even because had no predominant grass species — the ground was barren on many spots —, and as they belonged to another community they were neglected from the following enumeration. Thereafter two local maxima were found to exist at relevés 4–5 and 15–16. Between these maxima diversity as a trend shows a moderate decrease. After relevé 16 this decrease becomes definite.

The DIVDROP run (with the automatic selector described previously) resulted 10 plots of “reduced” diversities of the 10 selected species (total number of species was 82). First we grouped the species into two: **Group A** — Species having a general effect on the trend of diversity. Two species belonged to this group, *Brachypodium pinnatum* (L.) P. B. (Fig. 6) and *Festuca pseudodalmatica* KRAJ. ex DOM. (Fig. 7). **Group B** — Species having no general effect on the trend. This group is divisible into three subgroups:

- a) Species having a general positive effect on diversity along the relevé series but not on its trend (i. e. removing data of a species of this kind from the data matrix will cause a small decrease uniformly in most of the relevés). There was only one species of this type (Fig. 11).
- b) Species having a local positive effect (i. e. omitting a species of this kind the diversity will decrease uniformly in a little sequence of relevés). Five species belonged to this group.
- c) Species having a positive effect mainly in the small salient diversity values deviating from the trend (Fig. 5 — relevés 7, 10 and 13), i. e. these species are responsible for such deviant diversity values. This group consisted of two species, one example is given in Fig. 12.

Having analysed the diversity of the relevé series in question it can be stated (1) two species were responsible for the characteristic trend of diversity along the relevé series: the members of the abovementioned group A. *Festuca pseudodalmatica* caused the local minimum at the middle of the relevé series; the *Brachypodium* species was responsible for the minimum at the end; the DIVDROP plots are well correlated with the quantity (coverage) of these species (Figs 9, 10); (2) some values deviating from the trend can be explained by the effect of the members of group B. c; (3) local minima in relevés 6, 14, 18—19 were due to the low species number (Fig. 8). (4) six from the 10 species selected had no systematic effect on the diversity of the relevé series, therefore they are of no interest in a study like this.

**Discussion** — Diversity of communities (individuals) consists of two components: species number (number of attributes) and evenness. In certain cases species number (as it might be an index of diversity as well) can give an explanation as to the diversity trend itself. If it is not the case, we must analyse the second element, evenness. DIVDROP can be put to this purpose. This method proved to be satisfactory for explaining certain diversity patterns of individuals consecutive in any way. However, sometimes DIVDROP cannot prove the effect of some species occurring in the individuals. In these cases either species number may have an own trend with a more or less uniform evenness or the diversity trend may be influenced by not a few but many species.

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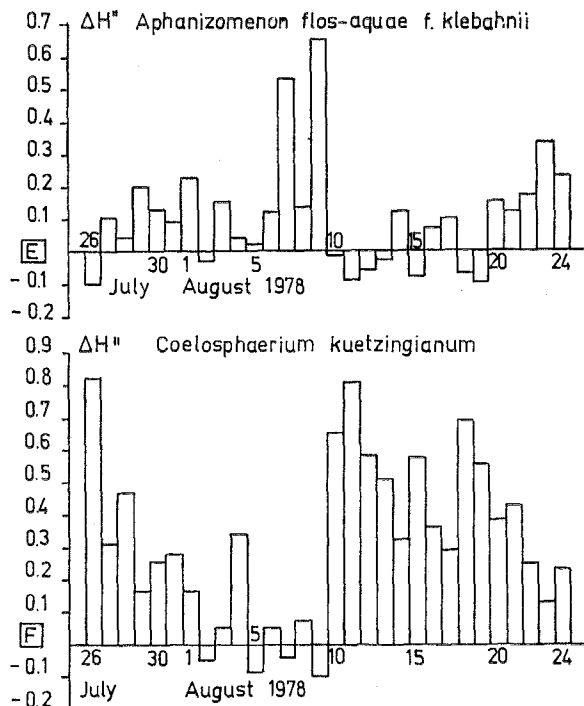
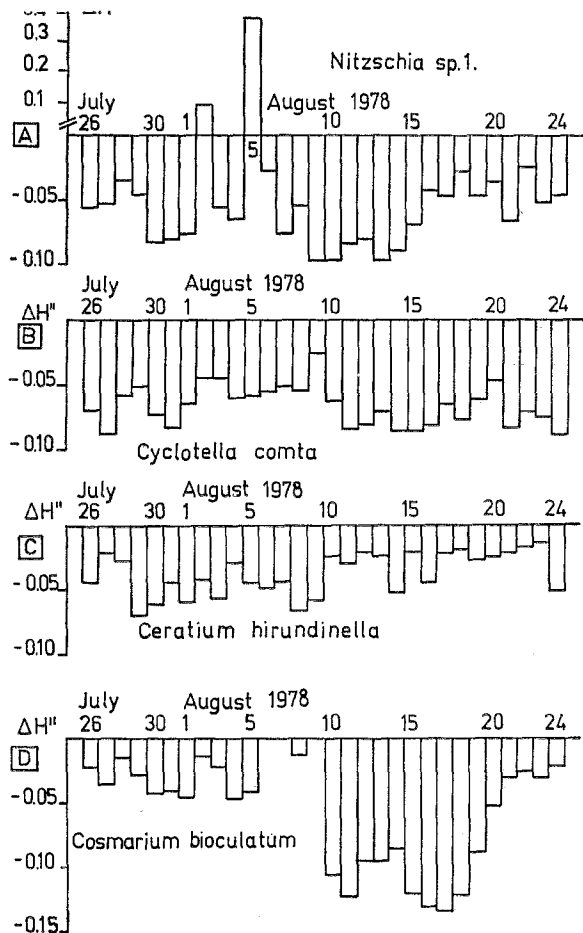


Fig. 1. Diversity differences ( $\Delta H''$ ) in some algal species. A=*Nitzschia* sp.1.; B=*Cyclotella comta* (EHRENB.) KUETZ.; C=*Ceratium hirundinella* (O. F. MUELLER) SCHRANK.; D=*Cosmarium bioculatum* (BRÉB.) RALFS; E=*Aphanizomenon flos-aquae* RALFS ex BORN. & FLAHL. f. *klebahnii* ELENK.; F=*Coelosphaerium kuetzingianum* NÄG.

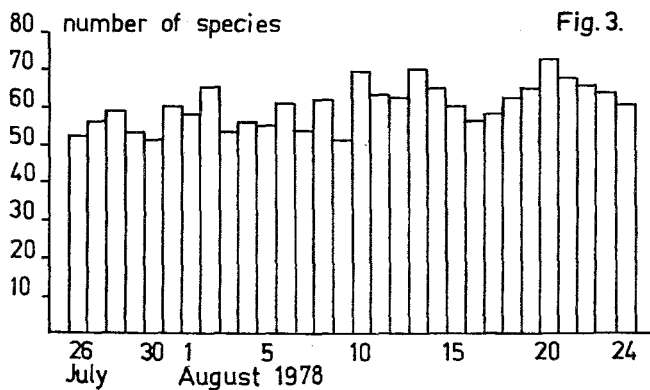
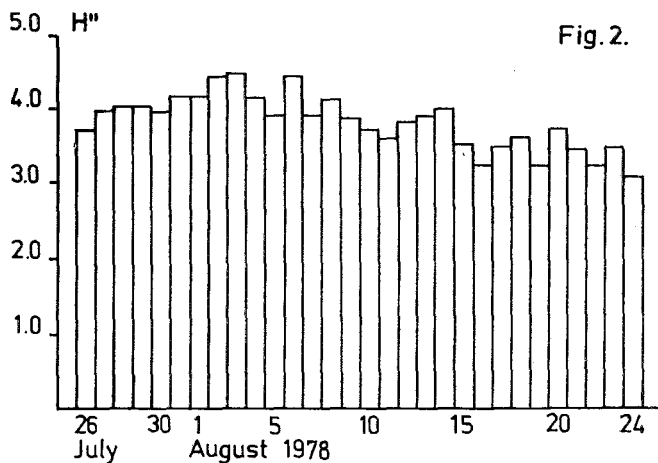


Fig. 2. Shannon diversity ( $H''$ ) of the samples. — Fig. 3. Number of species ( $s$ ) of the samples

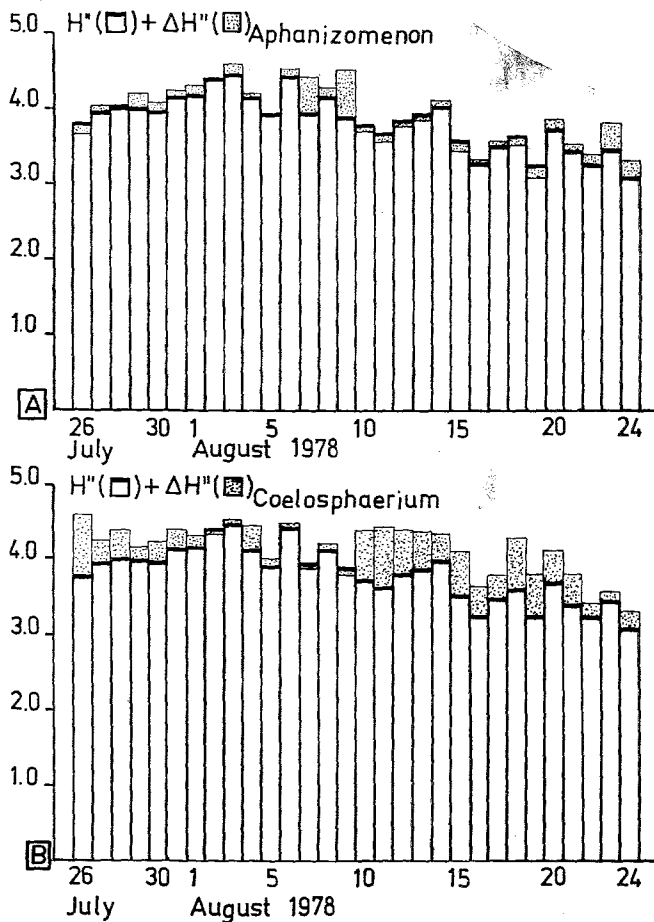


Fig. 4. Diversity and "reduced" diversity of the samples

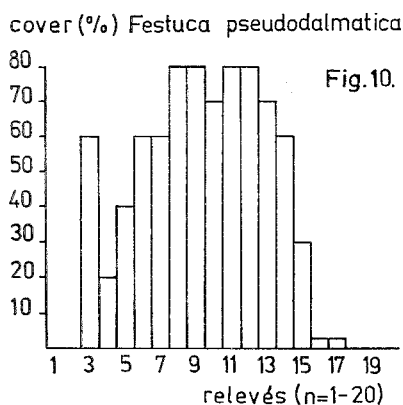
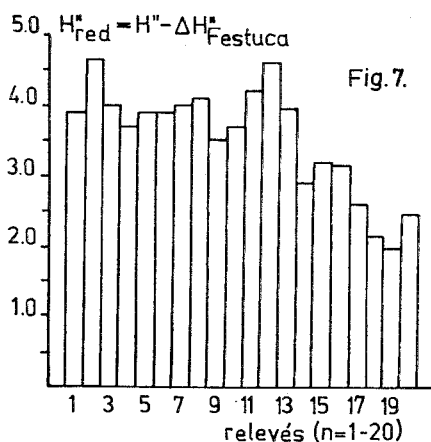
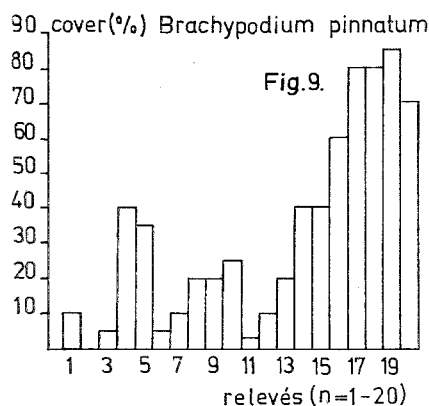
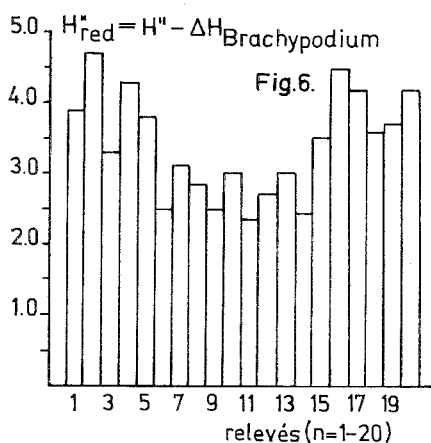
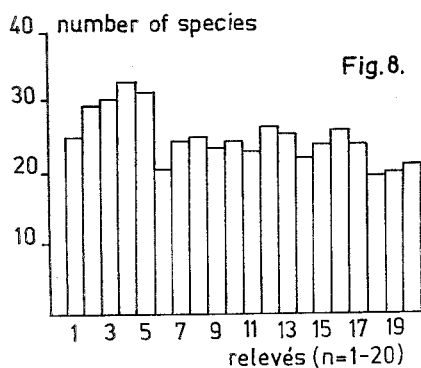
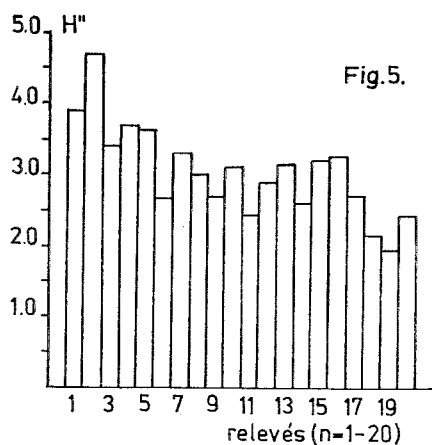


Fig. 5. Shannon diversity of the relevés ( $r$ ). — Fig. 6. "Reduced" diversity of the relevés after omitting the data of *Brachypodium pinnatum* (L.) P. B. — Fig. 7. "Reduced" diversity of the relevés after omitting the data of *Festuca pseudodalmatica* KRAJ. ex. DOM. — Fig. 8. Number of species of the relevés. — Fig. 9. Coverage values of *Brachypodium pinnatum* in the relevés. — Fig. 10. Coverage values of *Festuca pseudodalmatica* in the relevés



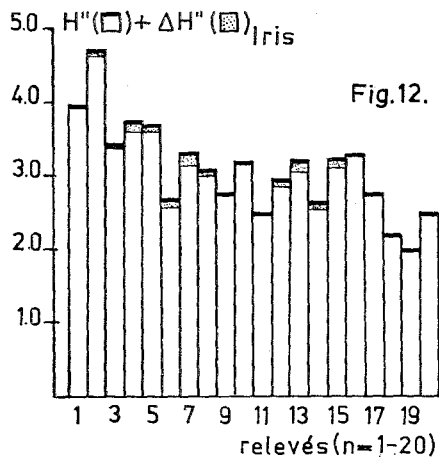
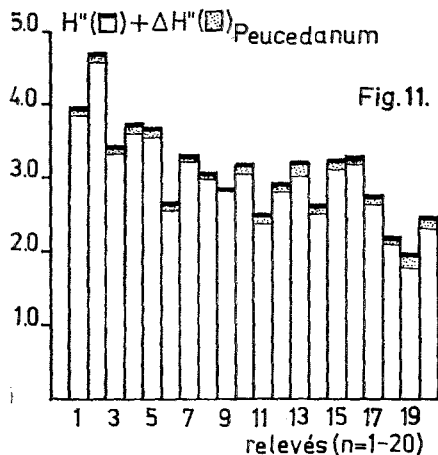


Fig. 11. Diversity and "reduced" diversity of the relevés in the case of *Peucedanum cervaria* (L.) Cuss. in LAP. — Fig. 12. Diversity and "reduced" diversity of the relevés in the case of *Iris variegata* L.